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SOLITARY AND SOCIAL OBJECT PLAY IN THE BOTTLENOSE DOLPHIN

(*TURSIOPS TRUNCATUS*)

by

Briana Marie Cappiello

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by Briana Marie Cappiello

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ABSTRACT

SOLITARY AND SOCIAL OBJECT PLAY IN THE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

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Many comparative studies have focused on the emergence of solitary and social play in early development. However, few consider observer and parallel forms of solitary play. In this study, use of video analysis revealed that there is a significant difference between the frequency of solitary, observer, parallel, and social object play states, in calf, juvenile, subadult, and adult bottlenose dolphins (*Tursiops truncatus*). While juveniles engaged in solitary play significantly more than any other age group, both juveniles and calves engaged in observer and social play significantly more than adults and subadults. Within their own age group, calves, juveniles, and subadults all showed a significant preference for solitary play. Preferences for play partners spanned across related or unrelated calves, juveniles, subadults, and adults. Calves preferred to play with juveniles, while juveniles preferred to play with both calves and juveniles. Juveniles preferred to play with calves during social play and with other juveniles during observer play. Calves and juveniles preferred unrelated partners. Similarly, calves and juveniles preferred to play with unrelated partners during observer play. Together, these results have implications for social learning and the transmission of behavior through observational play. With this knowledge, we can provide the appropriate social environment to captive individuals with limited or constrained social availability, increasing learning opportunities, so that individuals may develop more diverse behavioral repertoires while decreasing behavioral deficits.

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DEDICATION

I dedicate this thesis to my mentor Dr. Stan Kuczaj. It has been an honor to carry on part of your legacy studying cetacean play. I cherish the many lessons I have learned from you in academia as well as in life. It has been a privilege to be one of your students.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I - INTRODUCTION

Research concerning play in animals continues to gain popularity despite its questionable beginning. Play was dismissed as a valid construct by early researchers who considered play to be a result of boredom, neurosis, artifact, maturational immaturity, or misinterpreted functional behavior (Biben, 1982; Burghardt, 2014). While many had postulated that play was restricted to warm-blooded vertebrates equipped with a central nervous system, a large encephalization quotient, and parental care during early life stages (Bateson, 2014; Baumeister & Senders, 1989; Bekoff, 1984), observations of play behavior have been documented in terrestrial and marine mammals, avian species, reptiles, fish, insects, and cephalopods (Bateson, 2014; Bender, 2012; Burghardt, 2014; Dinets, 2015; Ford, 1983; Gamble & Cristol, 2002; Greene, Melillo-Sweeting, & Dudzinski, 2011; Hill & Ramirez, 2014; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Mackey, Makecha, & Kuczaj, 2014; Nunes, Sanchez, Hoffmeier, & Lancaster, 2004; Osvath, Osvath, & Bååth, 2014). Only in recent years, researchers have begun to identify the potential functions of play while also trying to understand its role in development from a comparative perspective.

Functions of Play

To determine the different functions of play, one must first define what play is. While considerations have included the structure and function of play, both features vary between species, according to their motivations, cognitive abilities, and biological roles (Bekoff, 1984; Kuczaj & Eskelinen, 2014). Although there is still controversy over defining play and identifying its functions, humans are able to identify play easily when considering five different characteristics: 1. Play is intrinsically motivating, so that performance in itself is a goal and is reinforcing; 2. Play provides a safe context to practice potentially risky or costly behaviors, while being protected from the consequences; 3. Role reversals and other changes in social relationships are common and are often accompanied by use of play signals that indicate that behavior is playful; 4. Play is repetitive, including modification of behaviors, so that they are exaggerated or fragmented, facilitating innovation and flexibility; 5. Play occurs when an individual is free from illness or stress, and is therefore an indicator of physiological and psychological well-being (Burghardt, 2005; Kuczaj et al., 2006).

Due to the inherent behavioral variability across age and species, play may serve different functions depending on the developmental period and specific species. As play peaks during juvenile years and declines in adulthood, it is suggested that play may be integral to physical and cognitive development (Bekoff, 1984; Burghardt, 2014). While many functions of play have been proposed, Bekoff (1984) organizes these functions into three overarching hypotheses that encompass a vast array of benefits that broadly correspond to motor training, socialization, and cognitive training functions.

Under the motor training hypothesis, an individual performs repetitive behaviors for the benefit of physical development. Through repeated movements and coordination of movements, one increases the effectiveness of different behaviors that are being practiced (Bekoff, 1984; Bender, 2012; Burghardt, 2005; Cheney, 1978). Associated with this hypothesis is the fine tuning hypothesis, during which risky behaviors are practiced under a play context, without associated costs or risks. Practicing fine motor movements under a safe context allows one to experience novel movements, as well as modify known motor patterns, expanding one's behavioral repertoire (Bekoff, 1984; Pellis & Pellis, 2007).

The social cohesion hypothesis suggests that play functions to establish and maintain social bonds (Bekoff, 1984; Cheney, 1978). Under this hypothesis, development of partner preference provides individuals of different ages and abilities, the opportunity to selectively interact with unfamiliar and familiar conspecifics. This selection allows individuals to acquire information about other conspecifics with which they may compete, cooperate, or form alliances, in the future (Bekoff, 1984; Cheney, 1978). Furthermore, different social skills such as turn-taking and dominance acquisition may be developed, providing the social cognition necessary for individuals to act appropriately with different conspecifics (Lee & Moss, 2014; Mackey et al., 2014). Forming and strengthening close bonds between conspecifics may reduce or delay dispersal in cohesive social species that live in mixed age social groups (Bekoff, 1984). However, in other species, such as African elephants (*Loxodonta africana*), males tend to disperse from their natal group after reaching maturity. Therefore, it has also been suggested that forming reliable bonds through social play may provide males with the social support needed for early dispersal (Lee & Moss, 2014).

A third proposed function of play, the cognitive training hypothesis, suggests that the motor development hypothesis and social cohesion hypothesis both shape behavioral development (Bekoff, 1984; Burghardt, 2014). Through play, individuals develop competence in responding to different features of the environment, simultaneously expanding their behavioral repertoires. These burgeoning repertoires likely result in greater behavioral flexibility, which would facilitate adaption to a changing environment.

Through the utilization of different behavioral strategies and methods, individuals now have a variety of problem-solving skills that can be applied across different contexts (Biben, 1982; Ford, 1983; Kuczaj et al., 2006). Similarly, as individuals interact and expand their social repertoire, their flexibility to adapt to changing social situations is enhanced. Ultimately, showing flexibility in social adaptations may have implications for stress resistance and emotional regulation, as individuals learn how to respond appropriately to different situations while managing both positive and negative outcomes of play with others (Bekoff, 1984; Kuczaj et al., 2006; Kuczaj & Horback, 2012).

Complexity of play is one indicator of environmental and social competence. By considering the complexity of different types of play, as well as the solitary and social states assumed, we are provided insight to the behavioral and social abilities of individuals as they age. Selectively choosing a play partner also allows individuals to control the complexity of play such as when older, more competent partners, are selected to challenge their abilities. Furthermore, examining partner preferences during different states of play may provide implications for behavioral transmission through social learning, indicating models from which individuals of different ages prefer to learn (Bender, 2012).

Types of Play

Two types of animal play have been documented, locomotor and object play. Each type of play differs in complexity and requires different cognitive capacities. By observing the type of play employed by individuals of different ages, we can determine at what age each type of play appears. Knowledge concerning the developmental trajectory of play can provide insight into the cognitive abilities of each age group through an examination of the complexity of their play (Bender, 2012).

Locomotor play is defined as exaggerated motor activity that is often repetitious, functionless, and is easily interrupted. Examples of locomotor play include variations of swinging, jumping, and chasing behaviors, as well as many other high intensity behaviors characterized by speed (Burghardt, 2005; Kuczaj & Eskelinen, 2014). This type of play is believed to allow for physiological strengthening and aiding the development of controlled coordinated movements. In doing so, individuals improve their efficiency, performing movements that may translate to hunting, mating, competitive, and antipredator behaviors (Burghardt, 2005; Kuczaj & Horback, 2012). Furthermore, by developing competency when performing different motor behaviors, individuals are able to properly orient themselves and coordinate their movements with others during social interactions, facilitating social competence and social cognitive development (Pellis & Pellis, 2007).

Object play is described as play behavior directed toward an inanimate object present in the environment (Bekoff, 1984; Burghardt, 2005). Through manipulating different objects, individuals gain knowledge about their surroundings, as well as features and properties that compose the objects in their environment (Biben, 1982; Ford, 1983; Kuczaj et al., 2006). While exploring novel objects can be stimulating, individuals can eventually habituate or become familiar, suggesting that the object is no longer as interesting as it was initially. However, individual play can become more complex and stimulating by manipulating objects in different ways, such as using different body parts (Baldwin & Baldwin, 1978). Engaging in object play under a social play context also provides additional complexity, as social object play requires a reciprocal relationship, adding an element of unpredictability and more complex cognition (Biben, 1982; Greene et al., 2011). By evaluating the way objects are manipulated, as well as the state under which object play occurs, we can chart cognitive development as object play increases in complexity (Belsky & Most, 1981; Bender, 2012).

Play States

While complexity of play varies according to the type of play employed, it is proposed that the solitary or social state assumed during play may have a similar effect. There are four different states of play, solitary, observer, parallel, and social, with each state providing different learning opportunities that can expand the behavioral repertoire (Bakeman & Brownlee, 1980; Bateson, 2014; Bender, 2012; Kuczaj et al., 2006). Solitary play involves an individual playing alone and was originally believed to indicate a lack of social ability. However, this interpretation does not hold as both solitary and social species engage in solitary play (Goldman, 1981) and it can be complex, allowing for the development of independence through interactions with the environment and innovation (Kuyk, Dazey, & Erwin, 1976). Other play states classified as solitary include observational and parallel play, as they lack direct interaction with others but occur within a social context (Bakeman & Brownlee, 1980; Goldman, 1981; Kuczaj & Horback, 2012). During observational play, an individual observes the play behaviors of another, which creates opportunities for observational learning and behavioral transmission (Goldman, 1981; Kuczaj et al., 2006). Parallel play occurs when one individual plays within proximity of another individual that is playing in a similar manner or with a similar object (Bakeman & Brownlee, 1980; Goldman, 1981). Previous studies conducted with human children suggest that parallel play functions as a means to transition from solitary to social play, by playing alongside each other (Bakeman & Brownlee, 1980; Baumeister & Senders, 1989). Therefore, certain play states may not reflect a required developmental phase but may be used to facilitate transition to a more complex play state, within a play bout (Bakeman & Brownlee, 1980).

When a play interaction between two individuals occurs, the play bout is classified as social. Social play has been defined as play behavior directed toward another living individual. Through interactions with familiar and unfamiliar conspecifics, play provides opportunity for the establishment and maintenance of social bonds, as well as the development of social skills (Bekoff, 1984; Cheney, 1978; Goldman, 1981). Similarly, these social play interactions likely enable individuals to learn about the abilities of future competitors, allies, and mates. By selecting specific partners (i.e., partner selectivity), individuals can increase the complexity of their play, as playing with older or more competent individuals should challenge their abilities (Bekoff, 1984; Cheney, 1978).

When provided with adequate social resources, partner preference may reflect the social cognitive abilities of the initiating individual (Bekoff, 1984). During juvenile years, many species of primates and other non-primate mammals display selectivity for same-aged peers. Playing with same-aged peers with similar abilities is hypothesized to allow young individuals opportunities to experience both winning and losing. As play can become frustrating and result in powerlessness or loss, it is possible that play may also have implications for stress resistance (Kuczaj et al., 2006). Many species prefer to play with same age peers, while species such as free-ranging baboons (*Papio Cyno-cephalus* *ursinus*; Cheney, 1978) and Belding's ground squirrels (*Spermophilus beldingi*; Nunes et al., 2004) prefer to play with their kin. Other species, like African elephants seek out novel play partners (Lee & Moss, 2014). However, when social availability is limited, the amount of time individuals spend playing, as well as the diversity of their play repertoire, may become limited (Baumeister & Senders, 1989; Kuczaj et al., 2006). The amount of early play exposure experienced may give rise to developmental differences due to the ability to observe and interact with other individuals (Bekoff, 1984; Bender, 2012; Mackey et al., 2014; Pellis & Pellis, 2007).

Overall, solitary and social play states reflect an increase in the complexity of play. Therefore, it may be expected that play states follow a linear developmental trend increasing in complexity with increasing levels of social participation, as suggested by Parten (1932). However, it has been argued that solitary and social play states do not correlate with age (Bakeman & Brownlee, 1980; Goldman, 1981). Many species exhibit social play within the first weeks of life while solitary forms of object play occur later in development and persist into adulthood (Lee & Moss, 2014; Mackey et al., 2014).

Play in the Bottlenose Dolphin

In captive and wild bottlenose dolphins (*Tursiops truncatus*), social play can occur as early as the first week of life. These interactions primarily occur between offspring and their mothers over the first two months, likely functioning to reinforce the maternal bond (Kuczaj et al., 2006; Mackey et al., 2014). Calves learn a variety of behaviors through observations of their mothers' activities, as well as other calves. However, as the frequency and complexity of play increases, calves become selective with their partners, displaying preferences for same-age peers rather than their mothers during play (Jones & Kuczaj, 2014; Kuczaj & Eskelinen, 2014). In fact, research has indicated that calves may acquire modified forms of behaviors previously learned from their mothers, during peer play (Kuczaj et al., 2006; McCowan, Marino, Vance, Walke, & Reiss, 2000).

As juvenile play among peers is most prevalent, it is suggested that peer play may also facilitate innovation, as well as the transmission of novel behaviors (Greene et al., 2011; Kuczaj et al., 2006). It has been found that juveniles are most likely to perform and imitate novel behavior from each other, only choosing to mimic unrelated adults in the absence of peers (Jones & Kuczaj, 2014; Kuczaj et al., 2006). Similarly, adults are also more likely to mimic novel and known behaviors from calves as opposed to other adults (Hill & Ramirez, 2014; Kuczaj et al., 2006). While imitation plays a role in social learning (Kuczaj et al., 2006), it is suggested that individuals may be playing to learn. By observing and replicating novel behavior, individuals learn new behaviors and provide a model for others. These behavioral patterns provide a method through which a novel behavior performed by one individual may spread throughout a social group (Kuczaj et al., 2006; Pace, 2000). Transmission of novel behavior through observational learning allows individuals to develop more diverse behavioral repertoires, providing a means to produce and utilize more innovative behavior and ultimately, greater behavioral flexibility (Gewalt, 1989; Kuczaj et al., 2006).

Due to the relationship between play and social learning, developmental differences in play behavior may be related to the social availability of play partners, specifically the opportunity to interact with more experienced juveniles (Bender, 2012; Mackey et al., 2014). This speculation is supported by the finding that young bottlenose dolphins will produce more complex behaviors at an earlier age if older peers are present in their environment (Kuczaj et al., 2006). Similarly, calves will produce more novel behaviors, if brought up in an environment with two or more calves present, as opposed to a calf lacking peers (Kuczaj et al., 2006). However, as calves age, their preference for playing with peers of the same age becomes less characteristic of their play interactions. Rather, calves may begin to select older and more experienced individuals to play with, as these conspecifics may challenge their abilities allowing the calves to increase their complexity of play (Baldwin & Baldwin, 1978; Kuczaj et al., 2006).

Another way to increase the complexity of play is to add a third partner or an object to a social interaction, creating triadic play (Tanner & Byrne, 2010). While social play occurs within the first week of life, calves have not been observed engaging in solitary object play until after the first few months. Therefore, it is believed that social and object-oriented abilities develop separately. While a slight decline in social play occurs as calves begin to explore different features and objects present in their environment, social play peaks again at the end of the calves first year of life. It is at this time that social and object-oriented abilities become integrated, allowing for triadic play interactions, including social object play (Greene et al., 2011).

Social object play involves individuals working together to initiate and maintain play resulting in increased play complexity. As play increases in complexity with increasing social participation, Parten (1932) hypothesized that developmental trends should follow suit. However, a study considering the prevalence of solitary and social play states in wild Atlantic spotted dolphins (*Stenella frontalis*) and captive bottlenose dolphins, found no significant difference between the play state assumed and age (Greene et al., 2011). Similar studies examining solitary and social play have been conducted on different species of dolphins and belugas (Greene et al., 2011; Hill & Ramirez, 2014). However, these studies did not consider observer and parallel states of play. While an increasing number of studies have been conducted on play development, systematic studies including social object play and all relevant states of play are lacking (Bender, 2012; Biben, 1982; Greene et al., 2011; Hill & Ramirez, 2014).

This study determined if the frequency of solitary, observer, parallel, and social object play states differed between and within calf, juvenile, subadult, and adult age classes. Additionally, preferences for playing with individuals of a specific age class or demographic relationship were explored overall and within observer, parallel, and social play states (Cheney, 1978; Lee & Moss, 2014; Nunes et al., 2004). As object-oriented and social abilities become integrated at the end of a calf's first year of life, it was predicted that parallel play would be most prevalent between unrelated calves. While solitary and social play reach their peak during juvenile years, characterized by high rates of innovation, it was predicted that solitary, observer, and social play states would be most apparent between unrelated juvenile peers.

CHAPTER II – METHODS

Subjects and Facility

Video recordings occurred at the Roatan Institute for Marine Sciences in Roatan, Honduras, where dolphins were housed on the north side of Bailey's Key. The enclosure consisted of a sea pen with a surface area of approximately 300 m^2, with depths reaching up to 7 m. The focal subjects of this study consisted of 30 bottlenose dolphins, 15 males and 15 females, ranging in age from 1 to approximately 24 years old (Table 1).

Table 1

Demographic Information for RIMS dolphins

Name	Sex	Birthday	Age Class
Champ	M	07/05/12	Calf
Lenca	M	07/27/12	Calf
Callie	F	07/28/12	Calf
Ellie	F	07/31/12	Calf
Polly	F	07/25/11	Calf
Tilly	F	08/14/11	Calf
Cortez	M	05/02/10	Calf
Mickey	M	07/11/09	Calf/Juvenile
Vin	M	08/04/09	Calf/Juvenile
Pigeon	F	08/13/09	Calf/Juvenile
Dixon	M	09/04/07	Juvenile
Margarita	F	08/14/07	Juvenile
Anthony	M	10/01/05	Juvenile/Subadult
Bailey	F	10/13/05	Juvenile/Subadult
Mr. French	M	08/13/04	Subadult
Ken	M	09/30/04	Subadult
Alita	F	07/06/03	Subadult
Fiona	F	10/25/03	Subadult
Ronnie	M	11/10/02	Subadult/Adult
Maury	F	01/14/02	Subadult/Adult
Han	M	05/02/09 c.d.	Adult
Hector	M	07/06/03 c.d.	Adult
Carmella	F	10/30/03 c.d.	Adult
Ritchie	M	10/30/03 c.d.	Adult
Bill	M	12/16/01	Adult
Mika	F	08/20/01	Adult

Table 1 Continued

Gracie	F	09/29/98 c.d.	Adult
Mrs. Beasley	F	12/04/98 c.d.	Adult
Cedena	F	10/03/90 c.d.	Adult
Paya	M	10/30/89 c.d	Adult

Note: c.d. = capture date

Data Collection

Data were collected during the months of January, March, May, June, July, and August, of 2012, and January, February, March, and May, of 2013. Collection occurred during early morning hours when all dolphins were together in the same enclosure. The archived video recordings were collected utilizing an underwater visual and auditory camcorder, using focal-animal, focal-subgroup, all occurrence sampling, as individuals came into view (Altmann, 1974). Data collected totaled 21 hours, 46 minutes, and 23 seconds of recording, with videos averaging a length of 54 seconds.

Analysis

To analyze videos, all natural object play bouts with an identifiable focal individual were coded. During each play bout, the state each individual assumed during play was recorded, providing a frequency of occurrence for each state (Appendix 1). During solitary play, a play bout was initiated when an individual directly manipulated a natural object using a part of their body. During observational and parallel play states, a play bout began when the focal individual came within one body length of another individual or group of individuals, for a minimum of one full second. During observational states, the focal individual directed its gaze toward the individual playing, while remaining stationary or traveling with that individual. During social play states, a play bout began when an interaction between two individuals occurred, where one or both individuals possessed the object, or a part of the object of focus. Each play bout terminated when the play state discontinued, changed, or if the individual or object moved out of view for more than one second.

Each dolphin was identified utilizing sketches, and photographs that displayed rake marks and pregnancy states for each video time period. After identification, the age group of each dolphin, according to the date of the recording, was documented. Ages were grouped according to calf (1-3yrs), juvenile (4-7yrs), subadult (8-10yrs), and adult status (11+). The frequency of each play state, as well as any conspecific involved in observer, parallel, and social states were summed for that year, resulting in a cumulative value, so that calf, juvenile, and subadult age groups could be easily compared. Video recordings were coded by two observers and an inter-rater reliability was determined using a Pearson Correlation Coefficient. The inter-rater reliability was calculated to be 100% for behaviors and 99.6% for identification during the year 2012, and 100% for behaviors and 97.8% for identification during the year 2013.

Data were analyzed using the years 2012 and 2013 combined. Any individuals that changed age class from year to year were treated as independent observations. Data were analyzed using IBM SPSS Statistics 23. All tests conducted have a specific confidence interval according to the adjusted Bonferroni alpha calculated to control for experiment-wise error. All data were entered into an Excel © sheet for analysis. One-way ANOVAs were used to determine if there was a significant difference between age class and the time spent playing. Chi Square Goodness of Fit Tests were performed on categorical data to determine if there was a significant difference in the frequency of solitary, observer, parallel, and social object play states between age classes and within each age class individually: calf, juvenile, subadult, and adult bottlenose dolphins. Chi Square Goodness of Fit Tests were also used to determine if individuals displayed a significant preference for play partners of a specific age class or demographic relationship, overall and within each play state. Tests of independence were not utilized due to a low number of observations for specific variable levels, which would have resulted in invalid tests. Post hoc descriptive analyses were utilized to determine if any individual differences influenced the results of the study.

CHAPTER III - RESULTS

To determine which age classes spent the most time playing, the duration of time individuals spent playing on screen was converted into a rate of play per minute and then into a percentage of the total time individuals played. The rate of play per minute did not significantly differ between age classes (Table 2). However, there was a significant difference between the percentage of time spent playing and age class (Table 3), with juveniles playing significantly more than both adults and subadults (Table 4), *F* (3, 13.115) = 3.99, $p < 0.05$. There was no significant difference between the percentage of time calves spent playing compared to juveniles, subadults, and adults.

Table 2

Descriptives: Rate of Play

	N	Mean	Std. Error	95% Confidence Interval for Mean	
				Lower Bound	Upper Bound
Calf	10	19.4690	5.00180	8.1541	30.7839
Juvenile	7	14.9014	2.58393	8.5788	21.2241
Subadult	8	12.3263	3.62929	3.7443	20.9082
Adult	12	8.6242	2.66080	2.7678	14.4805
Total	37	13.5432	1.91220	9.6651	17.4214

Table 3

Descriptives: Percentage Play

	N	Mean	Std. Error	95% Confidence Interval for Mean	
				Lower Bound	Upper Bound
Calf	10	.0320	.01397	.0004	.0636
Juvenile	7	.0700	.02795	.0016	.1384
Subadult	8	.0125	.00648	-.0028	.0278
Adult	12	.0075	.00250	.0020	.0130
Total	37	.0270	.00740	.0120	.0420

Table 4

Post Hoc Tukey HSD: Percentage Play

		Sig.	95% Confidence Interval	
			Lower Bound	Upper Bound
Calf	Juvenile	.242	-.0917	.0157
	Subadult	.739	-.0322	.0712
	Adult	.496	-.0221	.0711
Juvenile	Subadult	*.044	.0011	.1139
	Adult	*.013	.0107	.1143
Subadult	Adult	.993	-.0447	.0547

Note: *=Significance at an alpha of 0.05.

When analyzing differences between play states assumed and age class, juveniles (55%, $n = 113$) engaged in solitary play significantly more than all other age classes (calves: 30%, $n = 62$; subadults: 9%, $n = 18$; adults: 6%, $n = 13$), χ^2 (3) = 126.15, $p < 0.008$. Both calves (39%, $n = 29$) and juveniles (35%, $n = 26$) engaged in observer play significantly more than all other age classes (subadults: 4%, $n = 3$; adults: 22%, $n = 16$), χ^2 (3) = 22.32, $p < 0.008$. Calves (44%, $n = 16$) and juveniles (50%, $n = 18$) also engaged in social play significantly more than all other age classes (subadults: 6%, $n = 2$; adults: 0%, $n = 0$), χ^2 (2) = 12.66, $p < 0.008$. Adults were not observed engaging in social play.

When analyzing differences within age classes, calves (54%, $n = 62$) assumed a solitary play state significantly more than any other play state (observer: 25%, $n = 29$; parallel: 6%, $n = 7$; social: 14%, $n = 16$), χ (3) = 61.08, $p < 0.012$. Juveniles (69%, $n = 113$) assumed a solitary play state significantly more than any other play state (observer: 16%, $n = 26$; parallel: 4%, $n = 7$; social: 11%, $n = 18$), χ^2 (3) = 173.02, $p < 0.012$. Subadults (75%, $n = 18$) also assumed a solitary play state significantly more than any other play state (observer: 13%, $n = 3$; parallel: 4%, $n = 1$; social: 8%, $n = 2$), χ^2 (3) = 32.33, $p < 0.012$.

Overall, considering partner preference during play interactions, calves displayed a significant preference for playing with juveniles (66%, $n = 35$; calves: 19%, $n = 10$; subadults: 15%, $n = 8$; adults: 0%, $n = 0$), χ^2 (2) = 25.62, $p < 0.016$. Calves were not observed engaging in play with adults. Juveniles displayed a significant preference for playing with both calves (43%, $n = 22$) and juveniles (35%, $n = 18$; subadults: 16%, $n = 8$; adults: 6%, $n = 3$), χ^2 (3) = 18.09, $p < 0.016$. When analyzing partner preference by play state, calves' preference for playing with juveniles (59%, $n = 17$) during observational play approached significance when adjusted for experiment-wise error (calves: 21%, $n = 6$; subadults: 21%, $n = 6$; adults: 0%, $n = 0$), χ^2 (2) = 8.34, $p = 0.015$. Juveniles displayed a significant preference for playing with other juveniles (54%, $n = 14$) during observational play (calves: 15%, $n = 4$; subadults: 19%, $n = 5$; adults: 12%, $n = 3$), χ^2 (3) = 11.84, $p < 0.012$. Juveniles also displayed a significant preference for playing with calves (67%, $n = 12$) during social play (juveniles: 22%, $n = 4$; subadults: 11%, $n = 2$; adults: 0%, $n = 0$), χ^2 (2) = 9.33, $p < 0.012$.

When analyzing preferences for partners of a specific demographic relationship during play, calves displayed a significant preference for playing with unrelated individuals (94%, $n = 50$) versus related individuals (kin: 6%, $n = 3$; mother-calf: 0%, $n = 0$), χ^2 (1) = 41.67, $p < 0.016$. Juveniles also displayed a significant preference for playing with unrelated individuals (92%, $n = 47$) versus related individuals (kin: 8%, $n = 4$; mother-calf: 0%, $n = 0$), χ^2 (1) = 36.25, $p < 0.016$. When analyzing preferences for partners of a specific demographic relationship by play state, calves displayed a significant preference for playing with unrelated individuals (93%, $n = 27$) during observational play (kin: 7%, $n = 2$; mother-calf: 0%, $n = 0$), χ^2 (1) = 21.55, $p < 0.016$. Juveniles also displayed a significant preference for playing with unrelated individuals (89%, $n = 23$) during observational play (kin: 12%, $n = 3$; mother-calf: 0%, $n = 0$), χ^2 (1) = 15.38, $p < 0.016$. While related individuals include both kin and mother-calf relationships, no mother-calf preferences were observed.

CHAPTER IV – DISCUSSION

Play is expected to increase in complexity with age and social participation. However, it is unclear how play behaviors are transmitted during development. The goal of this study was to determine if there was a significant relationship between the frequency of solitary, observer, parallel, and social object play states, between and within different age classes. A second goal of the study was to determine if each age class displayed a significant preference for playing with partners of a specific age class or demographic relationship. The results of this study supported many of the proposed predictions.

Overall, the amount of time each age class spent engaging in play was consistent with previous findings (Greene et al., 2011). Juveniles engaged in play significantly more often than subadult and adult age classes. However, while juveniles spent more time playing than calves, and calves spent more time playing than subadults and adults, the difference was not significant. Additionally, when examining the age distributions for each play state, it was found that juveniles were more likely than any other age classes to engage in solitary play. Similarly, both calves and juveniles were more likely than subadults and adults to engage in observer and social play. Together, these results further support findings indicating that juveniles display the highest rates of play.

The first hypothesis was to determine if there was a significant difference between the frequency of solitary, observer, parallel, and social object play states, between and within calf, juvenile, subadult, and adult age classes. It was first predicted that parallel play would be most prevalent between calves. However, only eight instances of parallel play were documented. It is suggested that at the end of a calf's first year of life, social-and object-oriented abilities become integrated (Greene et al., 2011), which would facilitate the use of parallel play as calves begin to transfer object play abilities to social contexts. Within this sample of calves, only two individuals were nearing the end of their first year of life. This limited number of calves at this developmental stage may have restricted the opportunity to fully record the presence of parallel play. It is also possible that while many bouts of parallel play occurred between calves and juveniles the lack of parallel play was influenced by the social nature of bottlenose dolphins. Since bottlenose dolphins display social play within the first weeks of life, and triadic social play by the end of the first year of life, it is possible that parallel states of play are not needed to facilitate transition from solitary play to social play, as suggested by Bakeman and Brownlee (1980). Instead, it may be possible that previous experience with different types of social play may be enough to facilitate social object play, once an individual acquires the cognitive capacity to do so.

The second prediction was that solitary, observer, and social play would be most prevalent for juveniles. This prediction was supported, as juveniles engaged in solitary, observer, and social play significantly more than other age classes, except the calves, which also engaged in observer and social play significantly more than other age classes. This result should be expected, as the literature states that both solitary and social forms of play peak during juvenile years (Greene et al., 2011). One explanation for the lack of difference between calves and juveniles during observer and social play could be the way in which age classes were defined. Calves ranged in age from 1-3 years old while juveniles ranged in age from 4-7 years old. Since three of ten calves were approaching juvenile age and contributed to 28% of the calf play data, their rates of play may be more reflective of juvenile play, despite their chronological age classification. Similarly, since two of seven juveniles were approaching subadult age, we may have begun to observe decreased rates of play in these juveniles as they only contributed to 6% of the juvenile play data, despite their classification.

A second explanation for the lack of difference between calves and juveniles may be due to the influence of partner selectivity between calf and juvenile individuals. Overall, calves display a significant preference for playing with juveniles. Similarly, juveniles display a significant preference for playing with other calves and juveniles. Therefore, partner selectivity could be a driving force causing different age groups to engage in certain types of play. For example, as calves seek out juveniles to play with, calves may be solicited by juveniles to engage in social play specifically, as this is a state juveniles have a significant preference for assuming.

When considering partner selectivity according to state, juveniles displayed a significant preference for playing with other juveniles during observational play. Similarly, calves tended to prefer playing with juveniles during observational play, although this trend was not statistically significant. Observational play provides an opportunity to observe the behaviors of another conspecific playing. Through observation, an individual may learn to reproduce a behavior after viewing a model perform a given behavior. As imitation and observational learning are both forms of social learning, individuals may expand their behavioral repertoires. These findings suggest that calves and juveniles may engage in social learning through observational play. This conclusion is further supported by the finding that young individuals produce more complex behaviors at an earlier age if older peers are present in their environment

(Kuczaj et al., 2006). Given this, if individuals reside in an environment with constrained partner availability, individuals may lack the opportunity to play and learn from their preferred partners. As a result, individuals may also lack the opportunity to expand their behavioral repertoire, reducing their behavioral flexibility. As adults are more likely to mimic novel and known behaviors from calves as opposed to other adults, these findings have implications for the transmission of behaviors across age classes (Kuczaj et al., 2006; Hill & Ramirez, 2014).

When preferences for different play states were evaluated within age classes, calves, juveniles, and subadults engaged in solitary play significantly more than any other state. While this pattern is consistent across these age classes, the function of solitary play may vary according to age. As social play occurs after the first weeks of life, a slight decline in social play is observed before peaking again at the end of the calves first year of life, the same time at which object oriented and social abilities become integrated allowing for social object play (Greene et al., 2011). One explanation for solitary play preference is that it may be a necessity for calves to learn about their environment and develop object oriented skills before they have the capacity to engage in social play. As four of 10 calves in this study are under the age of one year, their preference for solitary play may be more pronounced, although these individuals only contributed to 12% of the calf play data. Similarly, engaging in solitary object play may allow individuals to gain more control over their movements, allowing them to practice orienting their bodies to different objects and surfaces. These orientation skills can then be translated to a social context under which individuals need to properly orient themselves to their conspecifics during play (Pellis & Pellis, 2007). As individuals over a year of age are still new to social object play, continuing to engage in solitary object play would allow them additional practice with orientation skills that increase in complexity particularly when a triadic context is introduced, requiring orientation to a conspecific and an object simultaneously.

Juveniles may engage in solitary play significantly more than any other state for similar reasons. As social play remains important in developing and maintaining social bonds, individuals may continue to engage in solitary play to continue honing skills that would be used socially (e.g., play signals to initiate and terminate social interactions, Bender, 2012; Kuczaj et al., 2006; Kuczaj & Eskelinen, 2014). However, as individuals approach subadult years, solitary play may change in function. Play decreases and motivation to play may change, such that solitary play may be used as stimulation while also maintaining specific skills that are needed to facilitate behaviors such as mating or foraging.

Previous research had indicated that partner preferences existed for different aged cetaceans (Greene et al., 2011; Hill & Ramirez, 2014). It was predicted that preferred play interactions would occur between unrelated calves and unrelated juveniles, respectively (Cheney, 1978; Lee & Moss, 2014; Nunes et al., 2004). Overall, this pattern was supported for both calves and juveniles. When examining partner preferences within each state, this pattern was supported for both calves and juveniles during observational play. Given that dolphins live in fission-fusion societies, learning to interact appropriately with unfamiliar dolphins would be advantageous in the future as potential relationships are built with repeated social interactions under playful contexts and information is acquired about future competitors and potentially, mates (Bekoff, 1984; Cheney, 1978; Lee & Moss, 2014).

Individual Differences

Post hoc descriptive analyses were performed to evaluate if individual differences accounted for the current findings. Although the sample size is large for cetacean research, it was still small enough that the influence of individuals could have impacted the results. Additionally, examining individual changes over time allowed any trends within age classes to be revealed.

When evaluating the play partners of individual calves, three of four calves that played exclusively with juveniles were individuals that aged from a calf to juvenile age class between the two years of data. Similarly, while nine out of 10 juveniles played with calves or other juveniles, two individuals also engaged in play with subadults, a third individual contributed two observations of play with only one subadult. Unlike the calves, only the individual that played exclusively with one subadult aged into the subadult class the following year and subsequently contributed two observations of play with two different adults. Although descriptive, it appears that individuals may have engaged in play with older partners to increase the complexity of their play. Upon becoming a subadult, this dolphin also displayed a decrease in partner selectivity when playing with adults, which may have been due to partner selectivity decreasing with age or that the number of adults willing to engage in play was more limited than before. The only other subadult that engaged in play was a male who played with a particular calf, and different juvenile individuals.

Play appeared to decrease with age as six of eight subadults and five of 12 adults did not engage in play. Of the remaining seven adults, three engaged in play exclusively with their calves. The other four adults engaged in very few instances of play, only two individuals contributed to more than one play bout.

Overall, younger age classes demonstrated greater partner selectivity. Older age classes decreased time spent playing but appeared to show greater diversity in partner selection. These trends need to be evaluated further with other samples given the limited sample sizes within the age classes and overall number of play events at each age class.

Limitations

One limitation concerns the inconsistent collection of the archival data. Data were collected over a series of months with recordings occurring one or two consecutive weeks each month. This data collection process may not have consistently captured age-related changes. Secondly, the time each individual or age group was recorded was randomly determined by the actions of the dolphin. This method of data collection can exclude dolphins that play but not within the camera's field of view. Similarly, it could over-represent individuals that spend more time with the camera or the camera operator.

All other limitations concern the sample of subjects. While individual differences were examined post hoc, findings may have been influenced by specific individuals due to the small sample size of each age class. Similarly, some age classes were better represented (i.e., calves: $n = 10$; adults: $n = 12$) while others were underrepresented (i.e., juveniles: $n = 7$; subadults: $n = 8$). Furthermore, the distribution of chronological ages included within the range of an age class, may have also had potential to influence the results for that age class.

A final limitation includes the potential constraint of available play partners during filming. For example, juveniles display a significant preference for engaging in social play with calves, who may not yet be of age or cognitive ability to engage in triadic social object play (Greene et al., 2011) or may be discouraged from play according to maternal parenting styles (Hill, Greer, Solangi, & Kuczaj, 2007; Kuczaj et al., 2006). As a result, juvenile individuals may have lacked opportunity for social play with calves and had the most opportunity for solitary object play. In older individuals, constraints of male alliances and the reproductive status of females may have had similar effects on availability of play partners (Greene et al., 2011; Kuczaj et al., 2006).

Future Directions

Future studies should strive to examine similar topics using a systematic, longitudinal approach. While grouping individuals by age was useful to determine general trends, the sample size for each age class was small, which may have allowed individual differences to influence the results of the study. Larger sample sizes within each age group may better reflect differences both between classes and within age classes. This method of analysis may be beneficial as developmental change may occur on a shorter time scale, as opposed to the span of years that defines an age class. Similarly, by making more frequent observations or observing subjects over a longer period of time, one increases the likelihood of observing less frequent forms of play, such as parallel, subadult, or adult play. Finally, using a focal follow approach of all individuals would increase the representation of animals that may not spontaneously play in front of a camera.

CHAPTER V – CONCLUSION

The purpose of this study to was to further explore solitary and social play in bottlenose dolphins by specifically examining two states of solitary play that have not been explored previously in cetacean literature, observer and parallel play. In doing so, this study evaluated the progression of different preferred play states throughout development, as well as the presence and progression of partner selectivity for individuals of different ages and demographic relationships. The results of this study are valuable, linking observer play and social learning processes during development, giving insight to the transmission of behavior throughout a social group.

This knowledge can be implemented to create more appropriate social environments for captive individuals with limited or constrained social availability. Individuals of different ages can experience learning opportunities with partners that can best facilitate the expansion of their behavioral repertoire, producing greater behavioral flexibility and cognitive stimulation. Furthermore, through development of a more diverse behavioral repertoire, stereotypical behavior and behavioral deficits should also decrease, resulting in more natural and enriching lifestyle.

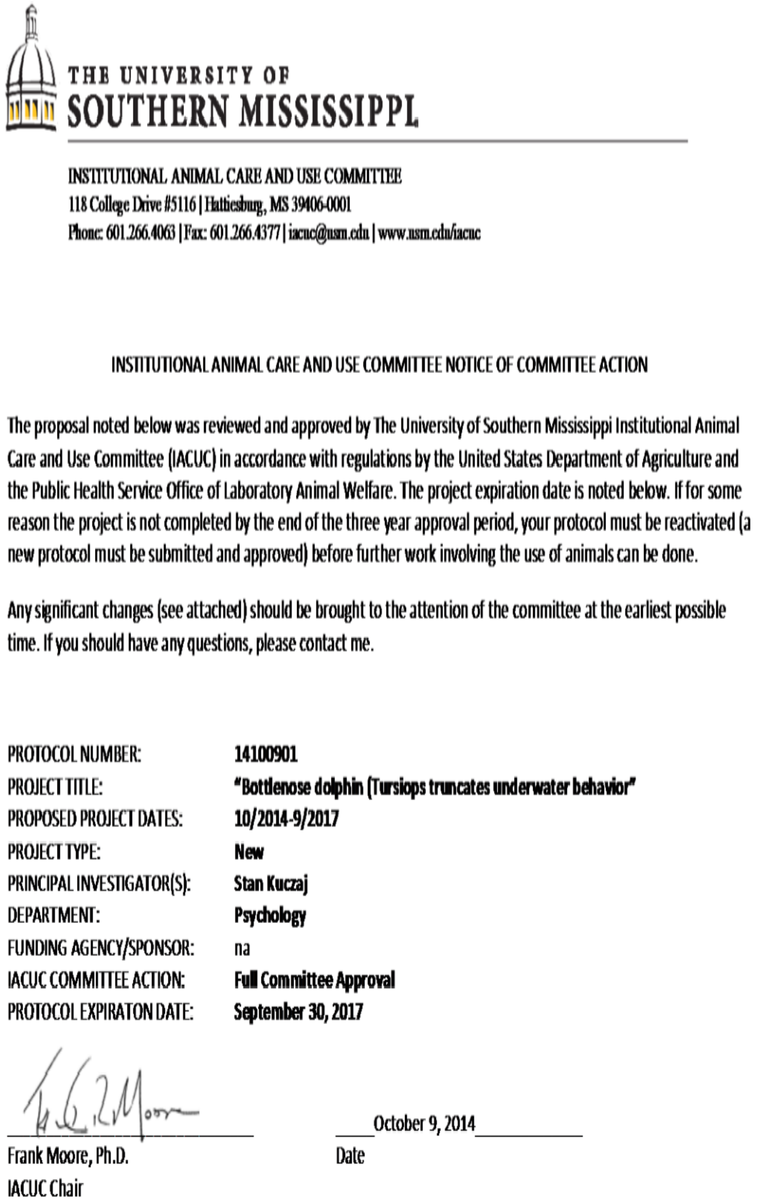
APPENDIX A - Ethogram

Table A1.

Operational Definitions of Behaviors

Code	Play State	Definition
SOL	Solitary	The individual directs play behavior at an object for a minimum of one second. No other individuals are actively interacting with the focal individual.
OBS	Observational	The individual is not interacting with an object or with another dolphin but is in sustained gaze of a particular conspecific or group of conspecifics interacting with an object. Individuals must be within one body lengths distance of each other for a minimum period of 1 second.
PAR	Parallel	The individual is interacting independently with an object, while an adjacent conspecific within one body lengths distance independently interacts with a similar object.
SOC	Social	The individual is interacting with a conspecific(s) within one body lengths distance. Social interactions include exaggerated or unpredictable motor patters, coordination of movements with a play partner(s) to manipulate the object of focus, chasing a partner(s) in possession of the object of focus, and passing or stealing the object of focus, to gain or maintain possession of the object.

APPENDIX B – Institutional Animal Care and Use Committee Notice of Committee Action



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INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:	**14100901**
PROJECT TITLE:	**"Bottlenose dolphin (Tursiops truncates underwater behavior"**
PROPOSED PROJECT DATES:	**10/2014-9/2017**
PROJECT TYPE:	**New**
PRINCIPAL INVESTIGATOR(S):	**Stan Kuczaj**
DEPARTMENT:	**Psychology**
FUNDING AGENCY/SPONSOR:	na
IACUC COMMITTEE ACTION:	**Full Committee Approval**
PROTOCOL EXPIRATON DATE:	**September 30, 2017**

Frank Moore, Ph.D.
IACUC Chair

October 9, 2014
Date

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